A GRAZING ECOTYPE IN A CHLOROPHYLLOUS ROOT-PARASITE, ORTHOCARPUS FAUCIBARBATUS SSP. ALBIDUS (SCROPHULARIACEAE)

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Abstract

A population of unusually short *Orthocarpus faucibarbatus* ssp. *albidus* plants in a closely grazed sheep pasture on the coast of northern California was studied. Branches were gently ascending and basal instead of erect from the upper stem. Seeds from this population were grown inland where wind buffeting, salt spray, cooler temperatures, close grazing, different host plants, and limiting soil were reduced or absent. The resulting plants closely resembled the parent population in both branching form and height. Shortness in this ecotype was due mostly to shorter rather than fewer internodes. Analysis of mean internode lengths in several coastal and inland populations showed significant differences between the grazing ecotype and all ungrazed populations, and between coastal and inland populations. Because this species is shade intolerant and an obligate outcrosser, close sheep grazing is beneficial in reducing the height of associated plants, allowing greater exposure to sunlight and insect pollinators. The harsh, spiny, rosette leaves of *Eryngium armatum* afford enough protection for the lower flowers and seed capsules of this herbaceous annual to prevent its demise through overgrazing.

Orthocarpus faucibarbatus ssp. *albidus* Keck is a white-flowered, herbaceous annual that is chlorophyllous and root-parasitic on a wide range of other vascular plants (Thurman, 1965).

In June, 1962, I noticed a population of very short *O. faucibarbatus* ssp. *albidus* in a closely grazed sheep pasture, 7.7 km south of Point Arena on the northern California coast (coded "SPC" below). At that time, relatively few ungrazed plants were available to demonstrate the normal heights for this colony. This is an area that has been grazed continuously for more than 100 years (Hektner and Foin, 1977). I revisited the site early in the season in May, 1964, before the pasture was grazed closely again. The ungrazed *O. faucibarbatus* ssp. *albidus* plants in the pasture and in an ungrazed area just outside of the fence were still much shorter than members of other populations of this subspecies, even those in other coastal populations, which are generally shorter than those inland. Most of the plants also had low, gently ascending branches originating close to the ground instead of a more erect branching from the upper stem characteristic of all other populations. This type of basal branching in ungrazed plants suggested genetic variation rather than morphological plasticity or a branching response to loss of the top of the plant by grazing.

Neel and Harris (1971) reported significant height reduction in *Liquidambar* and in corn (1972) when they simulated a shaking action similar to wind buffeting. Windblown salt aerosol was reported as an important cause for the low, prostrate form of *Baccharis pilularis* dominant at low coastal sites (Clayton, 1972). However, this still does

not explain why this *O. faucibarbatus* ssp. *albidus* population was so much shorter than other coastal populations exposed to these same general climatic factors.

The most noticeable difference in host plants seemed to be the abundance of *Eryngium armatum,* a member of the Umbelliferae with harsh, spiny, rosette leaves that were closely associated with many ungrazed *Orthocarpus* in the pasture. Kemp (1937) found a correlation of short strains of *Poa pratensis, Dactylis glomerata,* and *Trifolium repens* with closely grazed pastures. The natural selection of short plants that could persist among the spiny *Eryngium* leaves seemed a viable hypothesis.

Seeds from this short coastal population were planted inland in sites that were warmer, less windy, free from salt spray, ungrazed, and had different soils and host plants. The purpose of this experiment was to determine whether the observed shortness was due mainly to morphological plasticity in response to coastal environment conditions, to genetically fixed ecotypic variation, or to both.

Methods

About 200 seeds from the short-statured populations were sown on the soil surface of a marked plot in an abandoned orchard along state highway 29 in an Inner Coast Range valley 9 km north of Napa (SPI). This site was 60 km from the coast and 56 km from the nearest coastal population.

Although no *O. faucibarbatus* ssp. *albidus* were growing there, the orchard was considered a suitable site because it supported other species of *Orthocarpus* including *O. castillejoides,* which also occurred in the sheep pasture. Both coastal and inland *O. castillejoides* have a semiprostrate form characteristic of the species. Seeds from an *O. faucibarbatus* ssp. *albidus* population (5NN) 0.8 km south of the orchard test site were sown at SPI as a standard for the suitability and performance of *O. faucibarbatus* ssp. *albidus* at the test site. Weather records showed that the test site had 40 cm less precipitation (60 cm), 27 fewer rainy days (43), and 1.3°C warmer October to May mean temperature (11.9°C) than the parent site (SPC) during this growing season (U.S. Department of Commerce, 1964, 1965).

The sown plants at SPI were observed twice during the spring of the 1965 growing season and were collected on June 5, 1965, after growth had stopped and plants were dead. Considerable plot damage by off-road vehicles just prior to collection greatly reduced the number of plants available for analysis. However, the undamaged plants appeared to be a representative sample of the population as observed earlier.

Population samples from SPC and four other coastal populations (3SG, 8NB, 2NB, JCT) collected in May, 1964, were compared with the plants grown at the inland test site, i.e., from the short coastal

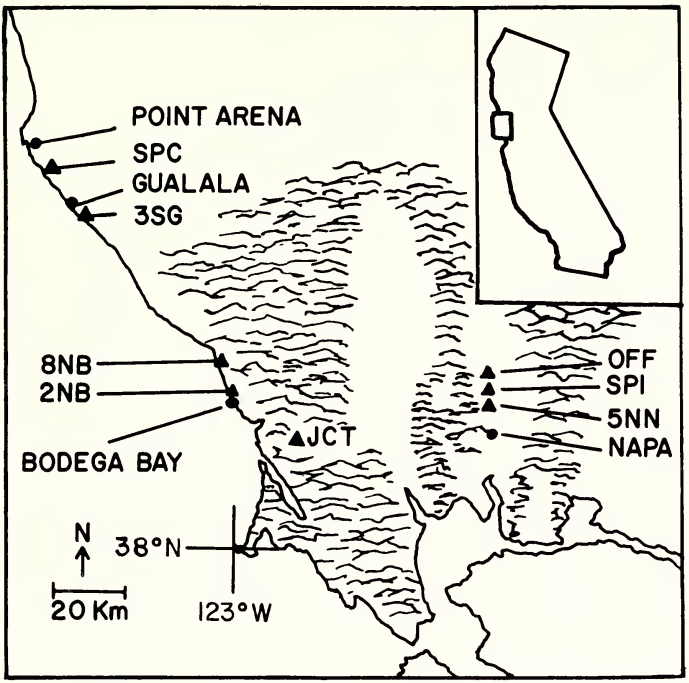

FIG. 1. Map of coastal California showing locations of the populations studied. SPC—short population in closely grazed sheep pasture 7.7 km S of Point Arena; 3SG—lightly grazed sheep range 4.8 km S of Gualala; 8NB—ungrazed roadside 12.9 km N of Bodega Bay; 2NB—ungrazed roadside 3.2 km N of Bodega Bay; JCT—lightly grazed cow pasture at junction of Dillion's Beach Rd. and Middle Rd.; 5NN—inland seed source 8 km N of Napa; SPI—seed from SPC population grown at the test site 8.9 km N of Napa; and OFF—*O. f.* ssp. *faucibarbatus* 9.7 km N of Napa.

seed source (SPI), and an inland seed source near the test site (5NN). An inland population of *O. faucibarbatus* ssp. *faucibarbatus* (OFF) from near the inland test site was also analyzed to compensate for the scarcity of *O. faucibarbatus* ssp. *albidus* plants in the inland test site. Except for flower color, the two subspecies differ little morphologically. Figure 1 shows the locations and symbols of the populations.

The number of internodes and the average internodal distance between the cotyledons and lowest flower were measured to learn whether the morphological basis of shortness was due to a reduced number of internodes, shorter internodes, or both. This is a more conservative measurement than total plant height which continues to increase as long as the plant flowers.

Two voucher specimens [*Thurman 647* (5NN) and *Thurman 711* (SPI)] are in UC. Further material is available from the author.

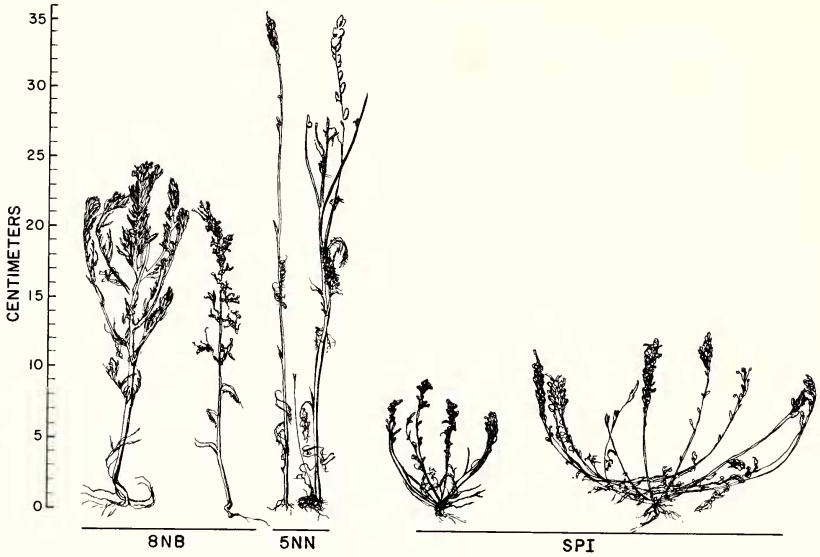

FIG. 2. Specimens of *Orthocarpus faucibarbatus* ssp. *albidus*. The left pair of plants was collected near the end of the growing season on an exposed coastal headland (8NB). The middle pair (5NN—from inland seed source) and right pair (SPI—seed from coastal sheep pasture) were harvested from the inland experimental site north of Napa at the end of the growing season.

Because variances were too heterogeneous to satisfy the assumptions for analysis of variance, the Student-Newman-Keuls test was used to determine which means were significantly different.

RESULTS

Seeds from the short, coastal sheep pasture population (SPC) when grown inland (SPI) produced plants with the same distinctive short central stem and ascending basal branches characteristic of their parent population. Figure 2 shows this growth form compared with representative plants from coastal (8NB) and inland (5NN) sites.

The mean lengths from cotyledons to lowest flower are shown in Fig. 3. The difference between SPC and the other four coastal and the two inland populations (5NN, OFF) was highly significant ($P < 0.01$). Although SPI was taller than its parent population (SPC), the difference was not significant. A highly significant difference ($P < 0.01$) was also found between the inland populations (5NN, OFF) and all others. The only other significant difference was between 2NB and 3SG ($P < 0.05$). Although 8NB had a mean height to lowest flower of 1.9 mm greater than 2NB, the smaller sample size reduced its statistical significance to slightly less than the 0.05 value.

Figure 3 shows the mean numbers and lengths of internodes, respec-

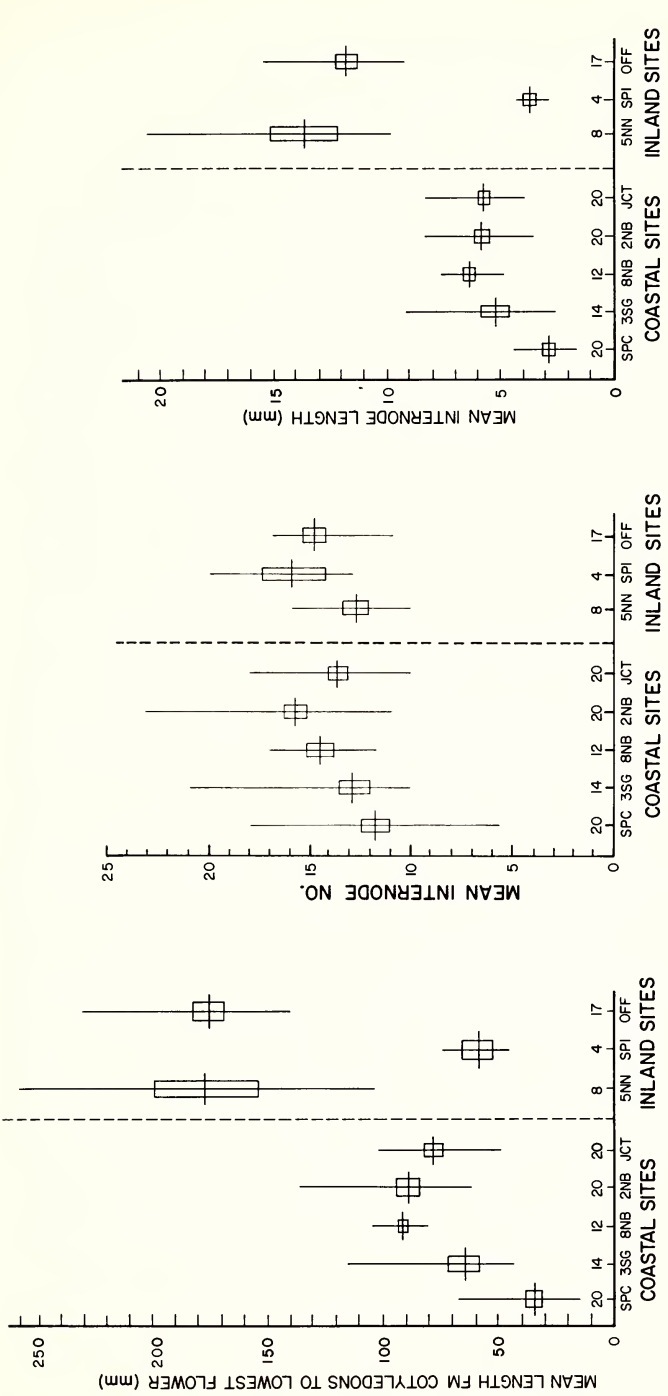

FIG. 3. Mean length of stem from cotyledons to the lowest flower, mean internode number, and mean internode length. Means shown as horizontal lines; ranges are shown as vertical lines; one standard error of the mean is shown on either side by open bars. Numbers above site designations are sample sizes.

tively, between the cotyledons and lowest flower. Mean internode lengths fall into three groups: inland (5NN, OFF), coastal (3SG, 8NB, 2 NB, JCT) and short, coastal sheep pasture, whether grown in place (SPC) or grown inland (SPI). The differences in internode lengths correspond more closely to the greater heights of the four other coastal and two inland populations than do the small differences in internode numbers. Most SPC plants had several very short basal internodes, about 3–5 mm long, a feature seldom found in other populations.

SPC differed significantly ($P < 0.05$) in internode number when compared with 2NB, 8NB, and OFF. Population 3SG was also found to differ significantly ($P < 0.05$) from 2NB in this respect.

The Student-Newman-Keuls test showed that the differences in internode lengths of 5NN and OFF and all other populations were highly significant ($P < 0.01$). The only other significant difference in internode length was between SPC and all except SPI and 3SG. The 3SG population was also in a sheep pasture but among lightly grazed bunch grasses.

Discussion

The production of the same basal, ascending branch form and short stature when seed of *O. faucibarbatus* ssp. *albidus* from the short, coastal sheep pasture (SPC) was grown under no grazing, on different soils, at higher temperature, with less wind and very little salt spray suggests a genetically fixed ecotype rather than a morphologically plastic ecophene. However, the slight increase in height of plants from SPC seed grown inland (SPI) is probably due to a plastic response to the reduced effects of coastal climatic factors.

The short coastal form (SPC) of *O. faucibarbatus* ssp. *albidus* has adaptive features similar to several Californian compositae described by Clausen and Hiesey (1958). Both *Layia jonesii* and *Hemizonia paniculata* also have marine ecotypes with shorter central stems and more spreading branches than their inland ecotypes. More extreme are *Layia platyglossa, L. chrysanthemoides,* and *Hemizonia multicaulis,* which have no central stem but only horizontal sidebranches attached to a central crown (Clausen and Hiesey, 1958). A similar response was reported in *Agrostis stolonifera* by Aston and Bradshaw (1966). Coastal climate is probably not responsible for the very short lower internodes and basal ascending branches in *O. faucibarbatus* ssp. *albidus* from SPC because the branching form of the other coastal populations is like that found in inland populations (Fig. 2).

However, the slightly shorter stature of most coastal populations is probably an adaptation to coastal conditions. Clausen and Hiesey (1958) suggest wind adaptation as a primary cause. Evidence by Neel and Harris (1971), in their studies of wind buffeting, revealed a significant reduction in number of nodes and in internode lengths in young *Liquidambar* trees when given only 30 seconds of moderate shaking daily.

They also found that corn treated similarly was 50 percent shorter and had 15 percent shorter internodes but resumed normal growth rates three days after shaking was stopped. Clayton (1972) suggested that salt aerosols in the wind are responsible for *Baccharis pilularis* being shorter (40–60 cm) on the shore than at a site one mile inland where the salt spray is less and plants are 2–3 m tall. Yet of the five coastal populations exposed to the same coastal climate, only SPC exhibited a noticeable reduction in height.

The morphological basis of shortness in coastal *O. faucibarbatus* ssp. *albidus* populations is due more to shorter internode length than to a reduced number of internodes (Fig. 3). The two populations with the greatest number of internodes are coastal (at least in origin of seed) rather than inland as expected in taller plants. In this respect, they resemble the coastal ecotypes in *Layia jonesii* and *Hemizonia paniculata* whose shortness is also due to shorter internodes (Clausen and Hiesey, 1958). Genotypes with shortening of only certain internodes have also been found. For example, Qualset et al. (1970) found short stature in a mutant of "Seneca" wheat where reduction was found only in the upper two internodes below the spike. However, a reduction of basal internodes appears to be more advantageous in *O. faucibarbatus* ssp. *albidus* by lowering the flowering branches into the spiny *Eryngium armatum* leaves, thereby reducing grazing loss.

Plant stunting, caused by small areas of unique soils such as serpentine (Kruckeberg, 1969) or an acid, podzolic soil like that underlying the pygmy forests nearby on the Mendocino coast (Jenny et al., 1969) could explain the localized nature of this phenomenon. Yet neither floristic analysis (Thurman, 1965) nor visual inspection indicated the presence of serpentine, acid, podzolic, or other unique soil condition at this site. The explanation for plants at SPC being significantly shorter than other coastal populations exposed to the same temperatures, winds, and salt spray appears to be more closely related to close grazing than to physical factors. Kemp (1937) found that short stature in *Poa pratensis, Dactylis glomerata,* and *Trifolium repens* persisted in turfs transplanted from closely grazed pastures to an experimental plot.

A second biological factor, protection by another plant from extinction due to grazing, is also suggested. Floristic analysis indicated that the persistence of *O. faucibarbatus* ssp. *albidus* easily could be due to the protection offered by *Eryngium armatum* (Umbelliferae) whose spiny, basal rosette leaves are 5–40 cm long and appeared to provide some protection from intense sheep grazing. A genotype for shortened internodes and basal, ascending branches that placed many flowers among the spiny leaves of *E. armatum* would have greater survival value because of the greater protection from sheep grazing than taller plants that branch from upper nodes. Consequently, the low form would contribute an increasingly larger proportion of seed than the

taller form. These annuals usually occur in small, discrete colonies, aiding rapid establishment of adaptive variants.

The same principle may apply to the shorter 3SG population in a lightly grazed sheep pasture where the coarse, unpalatable dead stems of two perennial bunch grasses, *Anthoxanthum odoratum* and *Danthonia californica*, may provide a similar protection from grazing.

The genotype for very short internodes in a site without close grazing would be detrimental to *O. faucibarbatus* ssp. *albidus* for two reasons. First, these plants tolerate very little shading. Greenhouse and garden studies (Thurman, 1965) showed that both transplanted seedlings and plants grown from seed became pale, spindly, and even died when their host plants shaded them. Although they are hemiparasites that rarely flower without root connections to a host, they could not depend entirely upon root parasitism and required ample sunlight for their own photosynthesis. Second, these *Orthocarpus* are self-incompatible and are dependent primarily on bees to open the corolla sac and transport pollen to another plant. Flowers occurring deep in vegetation are neither as conspicuous nor as accessible as the emergent form.

Thus, the short SPC form of *O. faucibarbatus* ssp. *albidus* is dependent both upon sheep to reduce the height of taller plants that would partially obstruct both pollinators and sunlight, and upon *Eryngium armatum* to help protect flowers and seed pods. Less severe sheep grazing would probably decrease the frequency of the grazing ecotype and favor the normal type found elsewhere on the coast.

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Literature Cited

Aston, J. L. and A. D. Bradshaw. 1966. Evolution in closely adjacent plant populations II. *Agrostis stolonifera* in maritime habitats. Heredity 21:649–664.

Clausen, J. and W. Hiesey. 1958. Experimental studies on the nature of species IV. Genetic structure of ecologic races. Publ. Carnegie Inst. Wash. 615.

Clayton, J. L. 1972. Salt spray and mineral cycling in two California coastal ecosystems. Ecology 52:74–81.

Hektner, M. M. and T. C. Foin. 1977. Vegetation analysis of a northern California coastal prairie: Sea Ranch, Sonoma County, California. Madroño 24:83–103.

Jenny, H., R. L. Arkley, and A. M. Schultz. 1969. The pygmy forest-podzol ecosystem and its dune associates of the Mendocino coast. Madroño 20:60–74.

Kemp, W. B. 1937. Natural selection within plant species as exemplified in a permanent pasture. Journal of Heredity 28:328–333.

Kruckeberg, A. R. 1969. Soil diversity and the distribution of plants, with examples from western North America. Madroño 20:129–154.

Neel, P. L. and R. W. Harris. 1971. Motion-induced inhibition of elongation and induction of dormancy in *Liquidambar*. Science 173:58–59.

———. 1972. Response to comments by D. F. Parkhurst and G. I. Pearman on

motion-induced inhibition of elongation and induction of dormancy in *Liquidambar*. Science 175:918–919.

QUALSET, C. D., G. N. FICK, M. S. CONSTANTIN, and T. S. OSBURN. 1970. Mutation in internode length affects wheat plant-type. Science 169:1090–1091.

SOKAL, R. R. and F. J. ROHLF. 1969. Biometry. W. H. Freeman & Co., San Francisco.

THURMAN, L. D. 1965. Genecological studies in *Orthocarpus*, subgenus *Triphysaria* (Scrophulariaceae). Ph.D. Dissertation, University of California, Berkeley.

U. S. DEPT. OF COMMERCE. 1964. Climatological Data, Vol. 68.

———. 1965. Climatological Data, Vol. 69.

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NOTES AND NEWS

PTERIDOLOGIA, A NEW MONOGRAPH SERIES

The American Fern Society is pleased to announce a new monograph series, PTERIDOLOGIA, which will publish monographs on ferns and fern-allies. The first issue will be devoted to Dr. David Wagner's "Systematics of Polystichum in Western North America North of Mexico." It is scheduled for publication during the spring of 1979. Publication will be on an irregular schedule, beginning at a rate of one or two monographs per year. All issues will be announced several months in advance of publication.

Dr. Alan R. Smith (University of California, Berkeley) has been appointed editor of PTERIDOLOGIA, in association with Prof. Donald R. Farrar (Iowa State University, Ames), Dr. David B. Lellinger (Smithsonian Institution, Washington), and Prof. Terry R. Webster (University of Connecticut, Storrs).

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